NeoBiota 81: 63–90 (2023)
doi: 10.3897/neobiota.81.95849
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities

Blanka Wiatrowska[1], Przemysław Kurek[2], Dawid Moroń[3], Waldemar Celary[4], Artur Chrzanowski[5], Paweł Trzciński[6], Łukasz Piechnik[7]

1 *Department of Botany and Forest Habitats, Poznań University of Life Sciences, Wojska Polskiego 71D, 60-625, Poznań, Poland* **2** *Department of Plant Ecology and Environmental Protection, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614, Poznań, Poland* **3** *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016, Kraków, Poland* **4** *Institute of Biology, Jan Kochanowski University, Uniwersytecka 7, 25-406, Kielce, Poland* **5** *Department of Forest Entomology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625, Poznań, Poland* **6** *Department of Monitoring and Signalling of Agrophages, Institute of Plant Protection, Władysława Węgorka 20, 60-318, Poznań, Poland* **7** *W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512, Kraków, Poland*

Corresponding author: Blanka Wiatrowska (blanka.wiatrowska@up.poznan.pl)

Academic editor: T. Knight | Received 30 September 2022 | Accepted 19 December 2022 | Published 23 January 2023

Citation: Wiatrowska B, Kurek P, Moroń D, Celary W, Chrzanowski A, Trzciński P, Piechnik Ł (2023) Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities. NeoBiota 81: 63–90. https://doi.org/10.3897/neobiota.81.95849

Abstract

Invasive plants directly and indirectly disrupt the ecosystem functioning, of which indirect effects, for example, through trophic cascades, are particularly difficult to predict. It is frequently assumed that the impact of an invading species on the ecosystem is proportional (linearly related) to its density or abundance in a habitat, but this assumption has rarely been tested. We hypothesised that abundance and richness of plants and potentially pollinators of wet meadows change as a result of invasion of steeplebush *Spiraea tomentosa* and that these changes are proportional to the density of the shrub. We selected 27 sites amongst wet meadows habitats invaded by *S. tomentosa* with coverage ranging from 0% to 100% and examined the diversity of plants, as well as the abundance and diversity of flower visitors (bees, butterflies with moths and flies). Our results showed that the richness of plants, as well as the richness and number of individuals of flower visitors, decrease significantly and linearly with an increase of the *S. tomentosa* cover. This finding supports the hypothesis that the impact of an invasive species can be proportional to their population density, especially if this species is limiting the available resources without supplying others. Our study is the first to show such an unequivocal negative, linear effect of an invasive shrub on the abundance

Copyright *Blanka Wiatrowska et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

and richness of potential pollinators. It proves that the negative impact of *S. tomentosa* on the wetland ecosystem appears even with a minor coverage of the invader, which should be taken into account when planning activities aimed at controlling the population of this transformer species. The simultaneously detected linear dependence allows us to assume that the benefits of controlling secondary populations of the shrub can be proportional to the incurred effort.

Keywords
bees, biodiversity, biological conservation, butterflies, flies, flower visitors, invasive plants, non-native species, wetlands

Introduction

Freshwater wetlands are important refuges for hygrophilous and hygrobiont plants and animals and, as such, they support diverse and unique species assemblages (Burke and Gibbons 1995). Nevertheless, in spite of the ecosystem services they provide, these types of ecosystems have been lost, degraded or strongly modified by human activities worldwide (Moroń et al. 2008; Davidson 2014; Reis et al. 2017). One of the most important reasons for their degradation are biological invasions, to which these ecosystems seem to be especially vulnerable (Zedler and Kercher 2004) due to frequent, large-scale disturbances, influx of nutrients, runoff of propagules flowing down the ground and accumulating in land depressions, as well as their limited connection over the network of corridors (Zedler and Kercher 2004; Fletcher et. al. 2019). Invasive plants disrupt the functioning of wetland ecosystems at different levels of their organisation both directly, for example, through competition for resources or changes in habitat conditions and indirectly, for example, through the trophic levels (Dibble et al. 2013; Mazurczyk and Brooks 2021). By initiating food chains, these plants can affect trophic interactions (Pearson 2009), which may initiate a trophic cascade (López-Núñez et al. 2017) manifested in population changes of consumers caused by direct and indirect relationships between them.

Amongst animals, insects are a group particularly sensitive to disturbances resulting from plant invasions (Van Hengstum et al. 2014; Schirmel et al. 2016), because they are highly dependent on plants as sources of food (Ehrlich and Raven 1964; Coley et al. 2006), shelter and breeding ground (Spafford et al. 2013). Therefore, the magnitude of response to changes in native flora composition caused by invasive plants varies extremely in different guilds of insects (Moragues and Traveset 2005; Fenesi et al. 2015). One of the crucial functions insects play in the ecosystem is pollination (Klein et al. 2007), which is the key in maintaining plant species diversity (Potts et al. 2010). However, data on the impact of invasive plants on pollinator populations are still scarce, whereas the effect of invasive plants on a pollinator community is equivocal (Bjerknes et al. 2007). Invasive plant species often compete with native ones for ecosystem services, such as pollination (Moragues and Traveset 2005; Larson et al. 2006; Bjerknes et al. 2007; Dietzsch et al. 2011; Williams et al. 2011). There are also known cases of pistil stigmas of native species being blocked by deposited foreign pollen,

which may limit the reproductive success of native plants (Brown et al. 2002; Larson et al. 2006). Nevertheless, invasive plants, due to their higher level of generalisation with regard to pollinators when compared to native plants, may also play new, important topological roles. For example, they attract pollinators to visit invaded ecosystems (Albrecht et al. 2014), increase the frequency of visits of pollinators on flowers of plants found in the same habitat (Bartomeus et al. 2008), increase pollinator populations, flight frequency and range (Moragues and Traveset 2005) and fill the seasonal resource gap in the native flora (Tepedino et al. 2008).

The direction of the impact of invasive plants on pollinators is strongly dependent on the scale of the invasion (Powell et al. 2013; Rejmánek and Stohlgren 2015). It is often assumed that the impact of invasive plants is proportional to their population density (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017), but, as noted by Elgersma and Ehrenfeld (2011), this assumption has been rarely tested and there is ample evidence that the effects of plant invasions on native pollinators are not linear (Moroń et al. 2019). Thus, the question arises whether the scenario of the non-linear effect of invaders on native plants and pollinators is a more general pattern. Therefore, in this study we assessed the impact of steeplebush on the species diversity of vascular plants, as well as the species number and diversity of pollinators in wet meadows.

The North American steeplebush (*Spiraea tomentosa* L., Rosaceae) is a highly invasive shrub found in central and northern Europe (Dajdok et al. 2011), with high potential for further spread (Wiatrowska et al. 2020). In the area of its natural occurrence, in the southern United States (USDA – The Plants Database 2022), *S. tomentosa* grows especially in wetland habitats and enters transitional and raised bogs (Reschke 1990; Schafale and Weakley 1990; Faber-Langendoen 2001). According to LaRosa et al. (2004), in its natural range, the shrub offers pollen and nectar as a reward for pollinators and, depending on the population density, it may have different (opposing) impacts on pollinators, such as bees (bumblebees) included in this study.

In Europe, *S. tomentosa* has been cultivated as an ornamental plant since the 18th century (Symes 1983). Currently this shrub is found in nine countries: Sweden, Germany, Poland, Belgium, Denmark, Norway, Croatia, Romania and Great Britain (Dajdok et al. 2011; GBIF 2022), while it is considered as an invasive species in five countries: Belgium (Invasive species of Belgium 2022), Denmark (Bruus et al. 2007), Germany (Balkenhol et al. 2018), Sweden (Tyler et al. 2015) and Poland (Dajdok et al. 2011; Tokarska-Guzik et al. 2012). In the area of its secondary occurrence, this shrub forms monodominant plant stands completely changing the structure and plant species composition of wetland communities – wet grasslands, lowland peat bogs or marsh forests (Dajdok et al. 2011; Wiatrowska and Danielewicz 2016) (Fig. 1).

However, still very little information is available on its effects on pollinators – flower visitors and the plant species composition. These data are urgently needed to communicate management priorities in times when invasions are a threat and challenge in nature conservation (Pyšek et al. 2020; Ricciardi et al. 2021; Moodley et al. 2022).

Spiraea tomentosa interacts with pollinators (LaRosa et al. 2004) and meets all four conditions (flower attraction, taxonomic affinity to native plants, formation of

dense populations and generalised pollination strategy) that, according to Bjerknes et al. (2007), make alien plants strong interactors for pollination in the area of their secondary range. The shrub was brought to Europe (Symes 1983; Hardtke and Ihl 2000) because it has stately inflorescences (Dajdok et al. 2011) that can be attractive to pollinators (Chittka and Schürkens 2001; Brown et al. 2002). The plant has a taxonomic affinity to *S. salicifolia* L. (Mirek et al. 2002) native to Central Europe, as well as many other *Spiraea* spp. common in cultivation (e.g. *S. douglasii* Hook. or *S.* ×*pseudosalicifolia* Silverside), which may facilitate attracting pollinators. Moreover, *S. tomentosa* develops denser and larger populations (Wiatrowska and Danielewicz 2016) than other species known as particularly attractive to pollinators (Ågren 1996; Mustajarvi et al. 2001; Thompson 2001). Probably, due to the relatively simple structure of flowers (*S. tomentosa* flowers are bisexual, 0.5–1.5 mm in diameter, with five free sepals, five petals orbiculate, free, usually light pink, five carpels and 15–20 stamens (Flora of North America 2022)), it also has a generalised pollination strategy, which means that it can attract many groups of pollinators.

Based on these premises, our main goal was to assess whether there was a relationship between the abundance of *S. tomentosa* and the diversity of plants, as well as the abundance and diversity of potential pollinators in wet meadow communities. We considered what influence the invader – non-linear or linear – has on plants and potential pollinators of indigenous communities. In the case of a non-linear relationship, the question arises whether there is a certain minimum point (tipping point), at which a pollinator population changes as the invasive plant becomes dominant.

We tested the hypotheses that: (1) the richness of plants and the abundance and richness of visiting pollinators change as a result of *Spiraea tomentosa* invasion and (2) changes are proportional (linearly) to the density of the shrub. The implementation of these studies was essential to provide insight into the density-dependent impact of the invasive alien species *S. tomentosa* on biodiversity, focusing on plants and pollinator species.

Figure 1. *Spiraea tomentosa* in wet meadows located in the Lower Silesian Forests (photo by B. Wiatrowska).

Methods

Study area

The research was carried out in a wet meadow complex located in the Lower Silesian Forests, in south-western Poland, where one of the first documented observations of *S. tomentosa* naturalisation in Europe was made (Fiek 1881; Schube 1903). Based on the water table (Bieroński et al. 2000a, b) and the present vegetation maps (Forest Data Bank 2022), we prepared distribution maps for wet meadows, where the soil is periodically saturated with water. The meadows are located in the same physical and geographic division (the Lower Silesian Forests mesoregion) (Solon et al. 2018) and have a similar geological history (Rzechowski 1994), climate (Woś 1999), soil properties and moisture conditions – the groundwater table is located just below the soil surface (Forest Data Bank 2022).

In the Lower Silesian Forests from the 1890s, large-scale drainage works were carried out, but after the Second World War, the maintenance of hydrotechnical structures was abandoned, which resulted in secondary bogging of the area (Bieroński et al. 2000a, b). Nowadays wet meadows are mainly maintained by regular management schemes, but *S. tomentosa* is spreading in many places (Wiatrowska and Danielewicz 2016). All studied meadows are dominated by *Molinia caerulea* (L.) Moench and *Juncus effusus* L. with numerous other native plants (Rutkowski 2011) suitable for pollinators (e.g. *Lythrum salicaria* L., *Lotus uliginosus* Schkuhr, *Cirsium palustre* (L.) Scop., *Filpendula ulmaria* (L.) Maxim., *Galium palustre* L., *Potentilla erecta* (L.) Raeusch, *P. reptans* L. or *Linaria vulgaris* Mill.) (Bělìn 1999; Buszko and Masłowski 2008).

In 2021, amongst six wet meadow complexes, 27 study sites were randomly selected for further analyses, each characterised with different *S. tomentosa* coverage. Wet meadows were at least 5000 ± 620 m apart, while the study sites located in the same meadow, but differing in *S. tomentosa* density, were at least 60 ± 42 m apart. To control the disruptive effects of the potential spatial gradients (distance from forests, human settlements, farmlands and meadows), we applied the Spearman test to make sure that these features did not correlate with steeplebush cover. We ensured that the selected study sites do not correlate with the distance of places to the closest forest areas (woodlands) (r_S = –0.08, p = 0.703), human settlements (r_S = 0.36, p = 0.069), farmland (r_S = 0.04, p = 0.844) and meadows (r_S = 0.14, p = 0.461). The distances were measured with QGIS 3.16 (QGIS Development Team 2022).

Surveys

In each of the study sites (n = 27), permanent circular plots of 100 m^2 were established. On each of these sites, the *S. tomentosa* cover was determined, a list of vascular plants was made and flower visitors were caught using a pan-trap placed in their centre. Data were collected during the period of full flowering of the shrub (Wiatrowska et al. 2018a) – in the second half of July and in August 2021.

The estimation of *S. tomentosa* coverage in the study sites was performed between 18 and 20 July 2021. Shrub cover was estimated visually using a cover class method (a modified Braun-Blanquet method) (Kercher et al. 2003), which provided reliable estimates for the dominant shrubs (Floyd and Anderson 1987). The coverage was estimated in classes with an accuracy of 10%, or less (every 0.5%), in the case of very low shrub densities (< 10%). The estimation consisted in an evaluation of what part of the study site is covered by all above-ground steeplebush organs jointly (e.g. shoots, leaves, flowers, fruits) by projecting them vertically on to the plane surface of the tested site. On all of the study sites, *S. tomentosa* cover ranged from 0% to 100% (47.6 ± 36.2%; mean ± SD) (see Appendix 1), where meadows completely free of the invasive shrub were taken as controls (0% invader coverage).

The plants species composition was surveyed twice (18–20 July and 27–29 August 2021) at each study site (n = 27) located in wet meadows at permanent circular plots (100 m^2). The vast majority of plant communities consisted of native species (74). However, in addition to *S. tomentosa*, the presence of single seedlings or juveniles of five other alien species was found (seedlings of *Prunus cerasifera*, *P. serotina*, *Quercus rubra* and juvenile of *Solidago canadensis* and *Juncus tenuis*). All the identified plant species, including *S. tomentosa*, were included in the analysis. Due to the fact that alien species other than *S. tomentosa* did not bloom during the field study, their presence was found on single sites and all had a negligible coverage (< 1%), thus it was assumed that they had no effect on flower visitors. Additionally, there was no relationship between *S. tomentosa* cover and the number of non-native species (generalised linear mixed-effects models; $t = -0.513$, $R^2 = 0.01$, $p = 0.618$). All plants were identified according to Rutkowski (2011).

Pan traps to catch insects (n = 27) were set up in the central part of each of the 27 study sites. This type of trap was used because they are an effective method of trapping insects in semi-natural habitats, including open areas with a wider field of vision (Mazon and Bordera 2008; Westphal et al. 2008; Acharya et al. 2021). Despite the limitations of the pan-trap method (Westphal et al. 2008; O'Connor et al. 2019), caused amongst others by their varying effectiveness in catching different groups of insects (Vrdoljak and Samways 2012), widely discussed perception of colour by insects (Briscoe and Chittka 2001; Song and Lee 2018; Van Der Kooi et al. 2021), including the colour of traps (Campbell and Hanula 2007; Vrdoljak and Samways 2012; Acharya et al. 2021), this method shows relevant effectiveness (O'Connor et al. 2019). Pan traps are useful for species that are active at night, trapping also rare or scarcely represented species. Their permanent presence in the field regardless of the temperature changes during daytime is of particular importance to obtain data on the complete species community, including specific weather conditions, during which, for example, bee flights take place (Borański 2015). According to premises presented above, one type of unicoloured, white traps were used to catch insects spontaneously attracted by the flowers of *S. tomentosa*. White pan traps are also commonly used in research on flower-visiting insects (Disney and Erzinclioglu 1982; Banaszak et al. 1994; Duelli et al. 1999; Campbell and Hanula 2007; Westphal et al. 2008; Vrdoljak and Samways 2012).

The traps were positioned in sunny places, on poles at the height of *S. tomentosa* inflorescences (ca. 70 cm above the ground and approx. 10 cm from the inflorescences of the shrub). The traps were 15 cm in diameter and filled to 2/3 volume with a mixture of water (95%), ethylene glycol (4.8%) and detergent (0.2%). Traps were first installed on 21 July 2021 and inspected three times at 14-day intervals during the peak of flowering and the peak of pollen season of this species. The samples were collected 03, 17 and 31 of August (exposure 21 July-03 August, 04 August-17 August, 18 August-31 August 2021), which made a total of 81 samples (pan traps). The caught insects were poured through a strainer and preserved in test tubes with 75% ethyl alcohol. Each selected group of flower visitors was identified according to Dathe (1980); Schmid-Egger and Scheuchl (1997); Pesenko et al. (2000); Pawlikowski and Celary (2003); Celary (2005); Scheuchl (2006); Bogusch and Straka (2012) – bees Apoidea Hymenoptera, Karsholt and Razowski (1996) – butterflies and moths Lepidoptera, Speight (2017) – flies Diptera.

Statistical analysis

All data analyses and visualisations were performed using the R ver. 4.2.1 software (R Development Core Team 2022). To verify the number of individuals and the species richness of potential pollinators, as well as plant species richness depending on *S. tomentosa* cover, we used the generalised linear mixed-effects models (GLMM) with a negative binomial distribution (bee abundance and species richness; butterfly and moth abundance and species richness, fly abundance) or Gaussian distribution (fly species richness, plant species richness) with the study meadow and site identities as the nested random factors. The models' assumptions were verified using the DHARMA ver. 0.4.6 package (Hartig and Lohse 2022). Additionally, models and results were provided applying GGEFFECTS ver. 1.1.4 (Lüdecke 2022), LME4 ver. 1.1-31 (Bates et al. 2022), LMERTEST ver. 3.3 (Kuznetsova et al. 2022) and MUMIN ver. 1.47.1 (Bartoń 2022) packages. The visualisations were performed using GGPLOT2 ver. 3.4.0 package (Wickham et al. 2022).

In addition, to understand if possible differences in the composition of potential pollinator communities depending on *S. tomentosa* cover are caused by pollinator species replacement or loss, we calculated the mean rank of the samples in a maximally packed matrix for overall pollinators: nestedness means that species-poor sites (i.e. those with a high rank in the nested matrix) are subsets of species-rich sites (those with a low rank). Data analyses and visualisation were performed using BIPARTITE ver. 2.18 (Dormann et al. 2022) and VEGAN ver.2.6-4 (Oksanen et al. 2022) packages.

We compared the rank of samples in the maximally packed matrix with GLMM (Gaussian distribution with the meadow and site identities as the nested random factors). The models' assumptions were verified using the DHARMA ver. 0.4.6 package (Hartig and Lohse 2022). Additionally, to obtain the models and results, we used GGEFFECTS ver. 1.1.4 (Lüdecke 2022), LME4 ver. 1.1-31 (Bates et al. 2022), LMERTEST ver. 3.3 (Kuznetsova et al. 2022) and MUMIN ver. 1.47.1 (Bartoń 2022) packages. The visualisations were performed using GGPLOT2 ver. 3.4.0 package (Wickham et al. 2022).

Results

During overall 27 216 hours of the pan-trap deployment, we collected 3649 individuals of 191 potential pollinator species or families (in the case of flies). Flies (Diptera) formed the most abundant pollinator group, accounting for 75% of all trapped insects. Butterflies and moths (Lepidoptera) comprised 15% of the collected insects. Bees (Apoidea, Hymenoptera) were only a minor fraction of flower visitors (10% of the specimens). A total of 80 vascular plant species were recorded in the investigated study sites (Table 1).

A negative relationship was found between steeplebush cover and plant species richness (t = –7.15; Fig. 2), with a 60% decrease of plant species richness.

An increase in *S. tomentosa* cover correlated also with a decline in the number of bee, butterfly and moth and fly individuals by about 70%, 80% and 45% (Fig. 3A–C), respectively (bees: Z = –4.77; butterflies and moths: Z = –7.54; flies: Z = –2.81). Similarly, bee, butterfly (and moth) and fly species richness decreased across the range of *S. tomentosa* cover by approx. 70%, 70% and 30% (Fig. 3D–E), respectively (bees: Z = –4.35; butterflies and moths: Z = –6.22; flies: t = –2.46).

The potential pollinator community in the habitats studied was significantly nested, indicating that species-poor samples (pan traps with a high rank) constituted subsets of species-rich samples (pan traps with a low rank) and that this pattern was not random. The nestedness rank significantly increased in proportion to *S. tomentosa* cover (t = 6.40; Fig. 4; see Appendix 2).

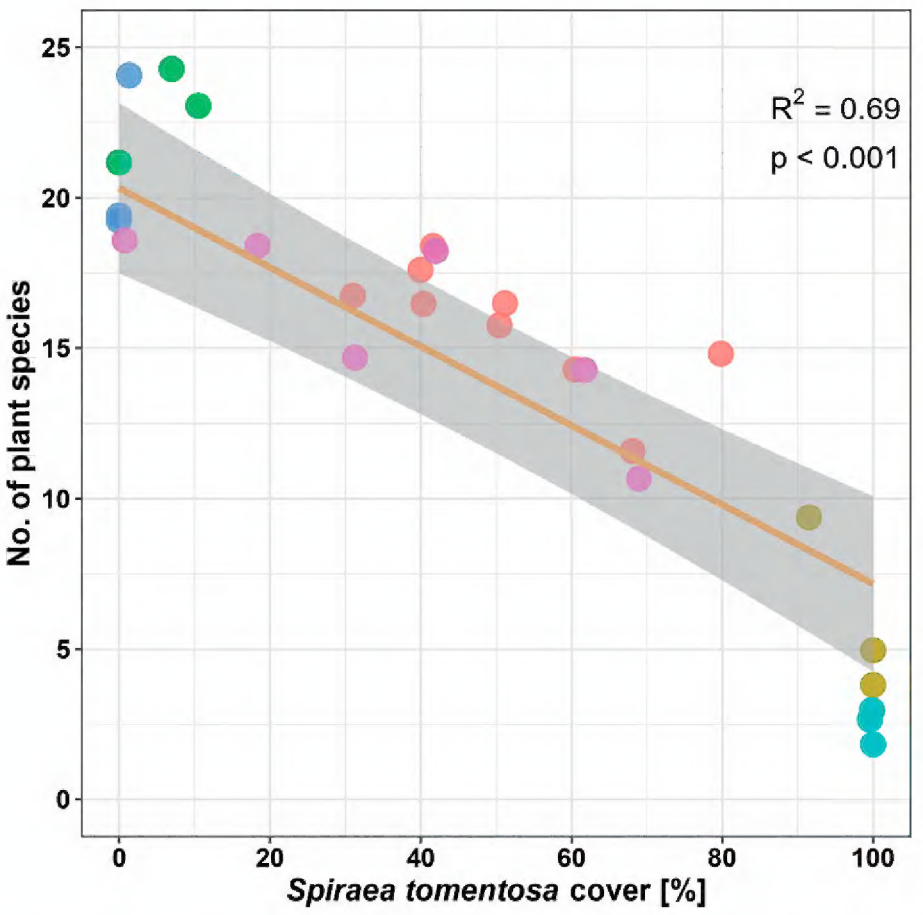

Figure 2. The relationship between species richness of plants and site cover by *Spiraea tomentosa*. Points represent each of 27 sites. Point colours correspond to a meadow. The 95% CI are marked with polygons. Jittering was added to aid visualisation.

Table 1. List of vascular plants and flower visitors found at study sites with their numbers.

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Achillea millefolium L.	*Ammophila sabulosa* (Linnaeus, 1758)	2	*Abrostola tripartita* (Hufnagel, 1766)	5	*Chalcosyrphus nemorum* (Fabricius, 1805)	2
Achillea ptarmica L.	*Andrena bimaculata* (Kirby, 1802)	1	*Abrostola triplasia* (Linnaeus, 1758)	1	*Cheilosia longula* (Zetterstedt, 1838)	1
Agrostis capilaris L.	*Andrena dorsata* (Kirby, 1802)	3	*Actinotia polyodon* (Clerck, 1759)	2	*Chloromyia formosa* Scopoli, 1763	1
Agrostis gigantea Roth	*Andrena flavipes* Panzer, 1799	3	*Agrotis segetum* (Denis & Schiffermüller, 1775)	4	*Chrysotoxum bicinctum* (Linnaeus, 1758)	3
Agrostis stolonifera L.	*Andrena minutula* (Kirby, 1802)	1	*Amphipoea oculea* (Linnaeus, 1761)	22	*Chrysotoxum festivum* (Linnaeus, 1758)	1
Alnus glutinosa (L.) Gaertn.	*Apis mellifera* Linnaeus, 1758	25	*Apamea monoglypha* (Hufnagel, 1766)	7	*Chrysotoxum verralli* Collin, 1940	3
Alopecurus pratensis L.	*Astata boops* (Schrank, 1781)	9	*Aphantopus hyperantus* (Linnaeus, 1758)	8	*Dasysyrphus tricinctus* (Fallen, 1817)	1
Angelica sylvestris L.	*Bombus bohemicus* Seidl, 1837	3	*Aporia crataegi* (Linnaeus, 1758)	1	*Episyrphus balteatus* (De Geer, 1776)	21
Athyrium filix-femina (L.) Roth	*Bombus jonellus* (Kirby, 1802)	2	*Araschnia levana* (Linnaeus, 1758)	8	*Eristalinus sepulhralis* (Linnaeus, 1758)	1
Betula pendula Roth	*Bombus lapidarius* (Linnaeus, 1758)	2	*Argynnis adippe* (Denis & Schiffermüller, 1775)	3	*Eristalis arbustorum* (Linnaeus, 1758)	11
Calamagrostis canescens (Weber) Roth	*Bombus lucorum* (Linnaeus, 1761)	17	*Argynnis aglaja* (Linnaeus, 1758)	3	*Eristalis lineata* (Harris, 1776)	3
Calamagrostis epigejos (L.) Roth	*Bombus pascuorum* (Scopoli, 1763)	24	*Argynnis paphia* (Linnaeus, 1758)	17	*Eristalis obscura* Loew, 1866	1
Campanula patula L.	*Bombus terrestris* (Linnaeus, 1758)	22	*Autographa gamma* Linnaeus, 1758	16	*Eristalis pertinax* (Scopoli, 1763)	3
Cardamine pratensis L.	*Colletes fodiens* (Geoffroy, 1785)	1	*Boloria selene* (Denis & Schiffermüller, 1775)	5	*Eristalis tenax* (Linnaeus, 1758)	14
Carex hirta L.	*Crabro cribrarius* (Linnaeus, 1758)	29	*Calophasia lunula* (Hufnagel, 1766)	1	*Helophilus hybridus* Loew, 1846	11
Carex ovalis Gooden.	*Crossocerus nigritus* (Lepeletier & Brülle, 1834)	1	*Carterocephalus palaemon* (Pallas, 1771)	1	*Helophilus pendulus* (Linnaeus, 1758)	6
Carex praecox Schreb.	*Dasypoda hirtipes* (Fabricius, 1793)	2	*Celaena leucostigma* (Hübner, 1808)	1	*Helophilus trivittatus* (Fabricius, 1805)	12
Cirsium arvense (L.) Scop.	*Ectemnius cephalotes* (Olivier, 1791)	1	*Cerapteryx graminis* (Linnaeus, 1758)	1	*Myathropa florea* (Linnaeus, 1758)	3
Cirsium palustre (L.) Scop.	*Ectemnius confinis* (Walker, 1871)	3	*Chiasmia clathrata* (Linnaeus, 1758)	2	*Oxycera leonina* (Panzer, 1798)	1
Deschampsia caespitosa (L.) P.B.	*Ectemnius continuus* (Fabricius, 1804)	44	*Coenonympha arcania* (Linnaeus, 1761)	1	*Parhelophilus versicolor* (Fabricius, 1794)	6
Dryopteris cartchusiana (Vill.) H.P.Fuchs	*Ectemnius lapidarius* (Panzer, 1804)	5	*Coenonympha glycerion* (Borkhausen, 1788)	1	*Scaeva pyrastri* (Linnaeus, 1758)	2
Epilobium palustre L.	*Ectemnius ruficornis* (Zetterstedt, 1838)	1	*Coenonympha pamphilus* (Linnaeus, 1758)	20	*Sericomyia silentis* (Harris, 1776)	1
Equisetum arvense L.	*Evylaeus albipes* (Fabricius, 1781)	3	*Cyclophora albipunctata* (Hufnagel, 1767)	1	*Sicus ferrugineus* (Linnaeus, 1761)	27
Festuca rubra L.	*Evylaeus calceatus* (Scopoli, 1763)	1	*Diachrysia chrysitis* (Linnaeus, 1758)	2	*Sphaerophoria scripta* (Linnaeus, 1758)	7
Filipendula ulmaria (L.) Maxim.	*Evylaeus laticeps* (Schenck, 1869)	1	*Diarsia brunnea* (Denis & Schiffermüller, 1775)	10	*Syritta pipiens* (Linnaeus, 1758)	9
Frangula alnus Mill.	*Evylaeus malachurus* (Kirby, 1802)	1	*Diarsia mendica* (Fabricius, 1775)	10	*Syrphus ribesii* (Linnaeus, 1758)	1
Galeopsis tetrachit L.	*Gorytes albidulus* (Lepeletier, 1832)	1	*Diarsia rubi* (Vieweg, 1790)	1	*Syrphus torvus* (Osten-Sacken, 1875)	3
Galeopsis bifida Boenn.	*Gorytes laticinctus* (Lepeletier, 1832)	2	*Dioryctria simplicella* Heinemann, 1863	1	*Tropidia scita* (Harris, 1780)	1
Galium aparine L.	*Gorytes quinquecinctus* (Fabricius, 1793)	2	*Endotricha flammealis* (Denis & Schiffermüller, 1775)	3	*Xylota segnis* (Linnaeus, 1758)	30
Galium palustre L.	*Halictus maculatus* Smith, 1848	1	*Epirrhoe alternata* (Müller, 1764)	8	*Xylota tarda* Meigen, 1822	15
Galium saxatile L.	*Halictus sexcinctus* (Fabricius, 1775)	3	*Euclidia glyphica* (Linnaeus, 1758)	2	Anthomyiidae	482
Galium uliginosum L.	*Hylaeus brevicornis* Nylander, 1852	1	*Eupithecia virgaureata* Doubleday, 1861	1	Calliphoridae	800
Glechoma hederacea L.	*Hylaeus cardioscapus* Cockerell, 1924	1	*Euxoa tritici* (Linnaeus, 1761)	1	Fanniidae, Muscidae, Scathophagidae	400
Holcus lanatus L.	*Hylaeus communis* Nylander, 1852	18	*Gonepteryx rhamni* (Linnaeus, 1758)	1	Rhinophoridae	156

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Holcus mollis L.	*Hylaeus confusus* Nylander, 1852	1	*Heliothis viriplaca* (Hufnagel, 1766)	1	Sarcophagidae	184
Hydrocotyle vulgaris L.	*Hylaeus difformis* (Eversmann, 1852)	2	*Hemaris fuciformis* (Linnaeus, 1758)	1	Tachinidae	530
Hypericum maculatum Crantz	*Hylaeus dilatatus* (Kirby, 1802)	1	*Hesperia comma* (Linnaeus, 1758)	33		
Juncus articulatus L.	*Hylaeus leptocephalus* (Morawitz, 1870)	1	*Hipparchia semele* (Linnaeus, 1758)	1		
Juncus effusus L.	*Hylaeus moricei luteifrons* (Strand, 1909)	1	*Hyloicus pinastri* (Linnaeus, 1758)	2		
Juncus tenuis Willd.	*Hylaeus pectoralis* Förster, 1871	5	*Hypena proboscidalis* (Linnaeus, 1758)	9		
Linaria vulgaris Mill.	*Lasioglossum leucozonium* (Schrank, 1781)	2	*Idaea aversata* (Linnaeus, 1758)	3		
Lotus uliginosus Schkuhr	*Lasioglossum zonulum* (Smith, 1848)	29	*Idaea emarginata* (Linnaeus, 1758)	1		
Lychnis flos-cuculi (L.) Greuter & Burdet	*Lestica clypeata* (Schreber, 1759)	1	*Inachis io* (Linnaeus, 1758)	1		
Lycopus europaeus L.	*Lindenius pygmaeus* (Van der Linden, 1829)	1	*Issoria lathonia* (Linnaeus, 1758)	1		
Lysimachia thyrsiflora L.	*Macropis europaea* Warncke, 1973	6	*Lacanobia oleracea* (Linnaeus, 1758)	2		
Lysimachia vulgaris L.	*Megachile centuncularis* (Linnaeus, 1758)	2	*Lacanobia suasa* (Denis & Schiffermuller, 1775)	1		
Lythrum salicaria L.	*Megachile ligniseca* (Kirby, 1802)	2	*Lycaena alciphron* (Rottemburg, 1775)	3		
Mentha arvensis L.	*Megachile versicolor* Smith, 1844	2	*Lycaena phlaeas* (Linnaeus, 1761)	4		
Molinia caerulea (L.) Moench	*Megachile willughbiella* (Kirby, 1802)	1	*Lycaena tityrus* (Poda, 1761)	2		
Peucedanum palustre (L.) Moench	*Melitta haemorrhoidalis* (Fabricius, 1775)	2	*Lycaena virgaureae* (Linnaeus, 1758)	43		
Phalaris arundinacea L.	*Nomada zonata* Panzer, 1798	1	*Lycophotia porphyrea* (Denis & Schiffermüller, 1775)	2		
Plantago lanceolata L.	*Oxybelus trispinosus* (Fabricius, 1787)	6	*Macaria alternata* (Denis & Schiffermüller, 1775)	3		
Poa pratensis L.	*Oxybelus uniglumis* (Linnaeus, 1758)	1	*Macaria liturata* (Clerck, 1759)	2		
Poa trivialis L.	*Pemphredon inornata* Say, 1824	1	*Mamestra brassicae* (Linnaeus, 1758)	2		
Polygonum hydropiper (L.) Delarbre	*Pemphredon lethifer* (Schuckard, 1837)	2	*Maniola jurtina* (Linnaeus, 1758)	64		
Populus tremula L.	*Pemphredon rugifer* (Dahlbom, 1845)	1	*Manuela complana* (Linnaeus, 1758)	3		
Potentilla anserina L.	*Philanthus triangulum* (Fabricius, 1775)	1	*Mecyna flavalis* (Denis & Schiffermüller, 1775)	3		
Potentilla erecta (L.) Raeusch	*Podalonia affinis* (Kirby, 1798)	1	*Melanargia galathea* (Linnaeus, 1758)	8		
Prunus cerasifera Ehrh.	*Seladonia tumulorum* (Linnaeus, 1758)	2	*Melanchra pisi* (Linnaeus, 1758)	2		
Prunus serotina Ehrh.	*Sphecodes hyalinatus* Hagens, 1882	1	*Mesapamea secalis* (Linnaeus, 1758)	2		
Quercus robur L.	*Sphecodes pellucidus* Smith, 1845	1	*Miltochrista miniata* (Forster, 1771)	3		
Quercus rubra L.	*Tachytes panzeri* Dufour, 1841	5	*Mythimna albipuncta* (Denis & Schiffermuller, 1775)	43		
Ranunculus repens L.	*Trypoxylon attenuatum* Smith, *1851*	3	*Mythimna ferrago* (Fabricius, 1787)	8		
Ranunculus acris L.	*Trypoxylon deceptorum* Antropov, 1991	2	*Mythimna pallens* (Linnaeus, 1758)	34		
Rubus idaeus L.	*Trypoxylon figulus* (Linnaeus, 1758)	9	*Noctua interjecta* Hübner, 1803	1		
Rubus plicatus Weihe & Nees			*Noctua pronuba* Linnaeus, 1758	3		
Rumex acetosa L.			*Nymphalis antiopa* (Linnaeus, 1758)	1		
Rumex acetosella L.			*Ochlodes venata* (Bremer & Grey, 1853)	1		
Salix aurita L.			*Oligia versicolor* (Borkhausen, 1792)	1		

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Scirpus sylvaticus L.			*Pandemis heparana* (Denis & Schiffermüller, 1775)	1		
Scutelaria galericulata L.			*Pelosia obtusa* (Herrich-Schäffer, 1847)	2		
Solanum dulcamara L.			*Perizoma alchemillata* (Linnaeus, 1758)	1		
Solidago canadensis L.			*Pieris brassicae* (Linnaeus, 1758)	5		
Sorbus aucuparia L.			*Pieris napi* (Linnaeus, 1758)	1		
Spiraea tomentosa L.			*Platyptilia nemoralis* Zeller, 1841	1		
Stellaria graminea L.			*Plusia festucae* (Linnaeus, 1758)	1		
Stellaria palustris Retz.			*Rusina ferruginea* (Esper, 1785)	1		
Urtica dioica L.			*Scopula immutata* (Linnaeus, 1758)	2		
Veronica chamaedrys L.			*Scotopteryx chenopodiata* (Linnaeus, 1758)	3		
Viola palustris L.			*Synaphe punctalis* (Fabricius, 1775)	1		
			Thalpophila matura (Hufnagel, 1766)	1		
			Thyatira batis (Linnaeus, 1758)	1		
			Timandra comae A. Schmidt, 1931	2		
			Tineola bisselliella (Hummel, 1823)	1		
			Vanessa atalanta (Linnaeus, 1758)	1		
			Xestia baja (Denis & Schiffermüller, 1775)	19		
			Xestia c-nigrum (Linnaeus, 1758)	13		
			Xestia ditrapezium (Denis & Schiffermüller, 1775)	25		
			Xestia stigmatica (Hübner 1813)	1		
			Xestia xanthographa (Denis & Schiffermüller, 1775)	16		

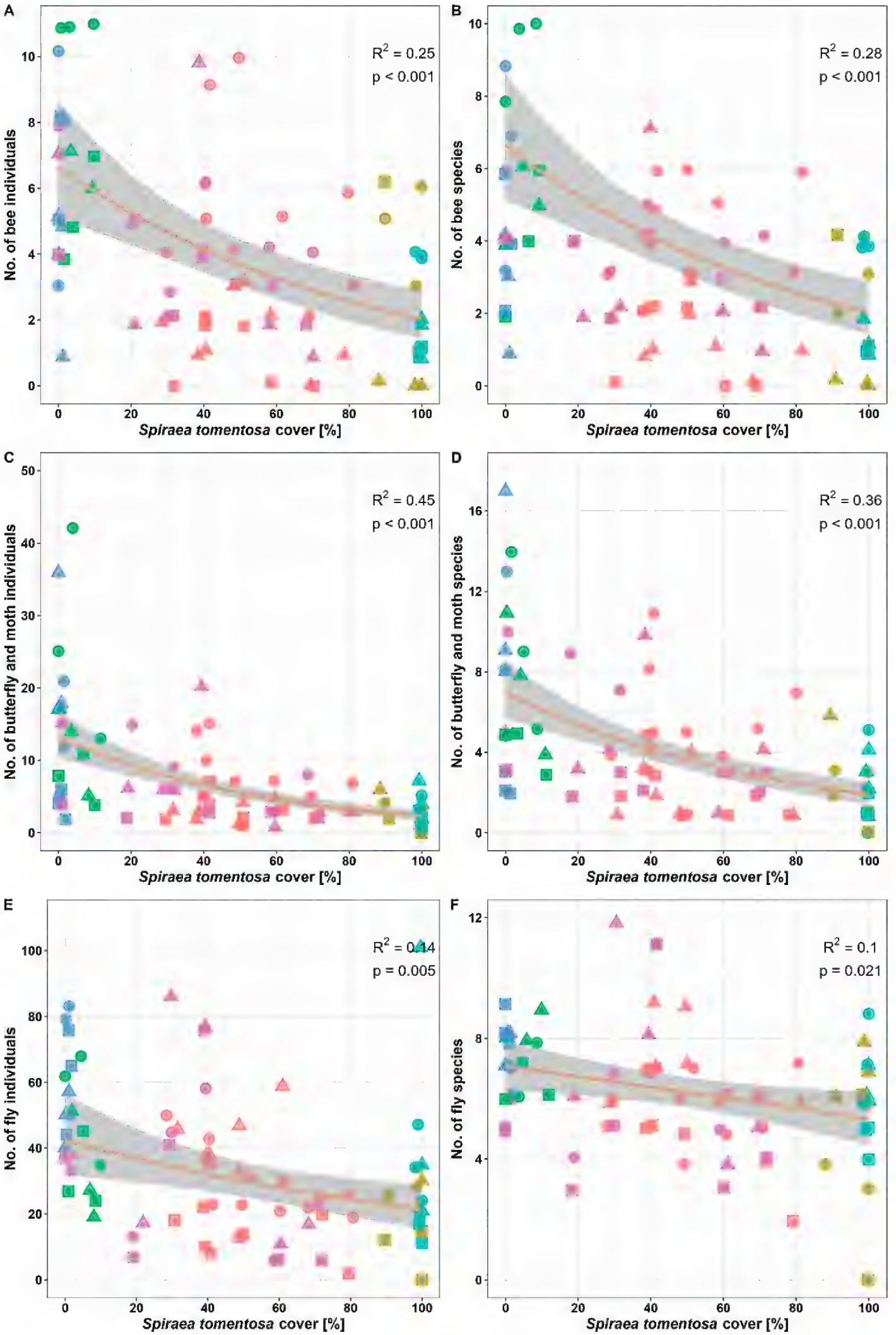

Figure 3. The relationship between abundance of **A** bees **C** butterflies and moths and **E** flies, as well as species richness of **B** bees **D** butterflies and moths **F** flies and site cover by *Spiraea tomentosa*. Points represent each of 81 surveys. Point colours correspond to a meadow and point shapes correspond to a survey number. Legend as in Fig. 2.

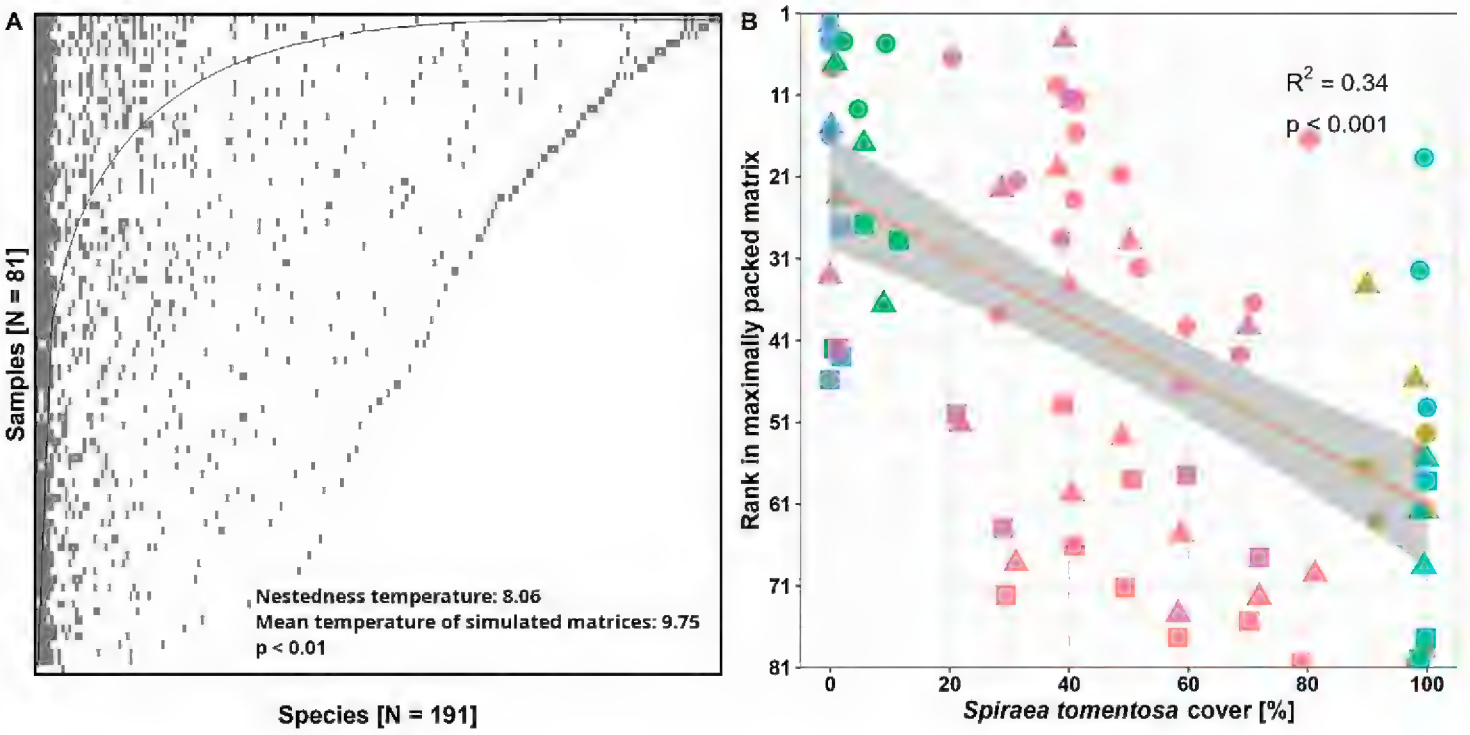

Figure 4. Nestedness structure of pollinator communities in the study sites **A** maximally packed matrix and **B** single ranks (points) for each pan trap depending on *Spiraea tomentosa* cover. Legend as in Fig. 2 and Fig. 3.

Discussion

The direction (negative vs. positive), the shape (linear vs. non-linear) and the strength of the relationship between the abundance of the invasive species and the diversity of native species determine which invaders pose the greatest threat to ecosystems (Bradley et al. 2019). It is often indicated that the impact of some invading species is proportional (linearly related) to its density or abundance in a habitat (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017; Sofaer et al. 2018), but there is also much evidence that the impact of other invaders may elicit a non-linear response from native species (Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017; Moroń et al. 2019).

In our research, we found a strong, negative, linear impact of the *Spiraea tomentosa* cover on vascular plant species richness, so this result positively validates the hypothesis. Our results showed that the diversity of plants decreased due to the increased invasive shrub coverage. These results correspond with a global meta-analysis that assessed the direction, shape and strength of the response of native communities to the increasing abundance of invasive species (Bradley et al. 2019). It was found that most often the impacts of invasive plants on native plant communities (at the same trophic level) are significantly negative and linear. However, the average impact of invasive plants on the diversity of native plants, estimated at 28% (Bradley et al. 2019), is much smaller than that shown for *S. tomentosa* in our research (60%).

In other studies on the impact of alien species on plant species richness, it was found that, amongst alien species entering wetlands in Central Europe, the invasion of *Mimulus guttatus* DC and *Impatiens glandulifera* Royle does not reduce the species richness of native plants. The invasion of *Solidago gigantea* Aiton and *Rudbeckia laciniata* L. decreases species richness by about 26% and 30%, while the invasion of *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, *F. japonica* (Houtt.) Ronse

Decraene and *F.* ×*bohemica* (Chrtek & Chrtková) JP Bailey contributes to the reduction of species richness by 86%, 73% and 66%, respectively (Hejda et al. 2009). Amongst the species entering wetlands, the impact of *S. tomentosa* on plants is, therefore, comparable to the impact of alien *Fallopia* sp. considered as an example of transformer species (Sukopp and Sukopp 1988; Cronk and Fuller 1995; Sukopp and Starfinger 1995), which changes the nature, condition and form or character of ecosystems (Richardson et al. 2000).

The direction, shape (linear vs. non-linear) and strength of the impact of an invasive plant species on insects, including potential pollinators, is more difficult to predict (Stout and Morales 2009; Lenda et al. 2010). When invasive species are at a lower trophic level, no consistent trend of impacts on native species or communities has been demonstrated (Bradley et al. 2019). This is due to the properties of environments that have different buffering potentials, for example, due to the condition of the recipient's native ecosystem (e.g. Mason and French (2007); Pyšek et al. (2012)), different redundancy of the food web (Gilbert and Levine 2013), as well as properties of the invasive species themselves. The role of the invasive species impact on pollinator assemblages is ambivalent – some of them increase the base for pollinators (Moragues and Traveset 2005; Bartomeus et al. 2008; Hejda et al. 2009; Stout and Morales 2009), while others may limit it (Vanbergen et al. 2018). Reducing plant diversity is considered to be a factor that is directly manifested in reduced food resources for pollinating insects (Potts et al. 2003; Moroń et al. 2008; Senapathi et al. 2015, 2017), but, as noted by Vanbergen et al. (2018), surprisingly little research unequivocally indicates the negative impact of invasive species on the diversity or abundance of pollinators.

In our research, we found a strong, negative, linear influence of *S. tomentosa* on the abundance and diversity of flower visitors, which allows us to positively verify our hypothesis regarding the negative effect of the shrub cover on potential pollinators.

Butterflies and moths seem to be least resistant to *S. tomentosa* infestation, as in dense populations of this shrub, the number of individuals decreased by 80% and species richness was reduced by 70%. The strong response of this group of insects is understandable, because Lepidoptera species strongly depend on plants throughout their life cycle – they use them for breeding and as a source of food for larvae and adults (Altermatt and Pearse 2011), resulting in their limited resistance to disturbance. Butterflies and moths have been shown to suffer from invasion, because alien plant species can replace beneficial native partners (Lenda et al. 2013; Trigos-Peral et al. 2018) and many butterfly species are recognised as food specialists, functionally constrained to exploiting a limited group of plants (Tallamy and Shropshire 2009), for which food source redundancy is relatively low (Moroń et al. 2019). Moreover, invasive plants due to their low nutritional value or toxicity may reduce their reproductive success and consequently lead to genetic bottlenecking (Davis and Cipollini 2014). Some of these plants can also affect the herbivores to become more attractive to predators (Bezemer et al. 2014). Although shoots and leaves of *S. tomentosa* can be used as a food source by a native moth species – *Earias clorana* larvae (Wiatrowska et al. 2018b), our results indicate that the buffering mechanism is not observed and butterflies, as well as moths, react quickly and very negatively to *S. tomentosa* invasion.

Other insects that have strong, often reciprocal, relationships with native species of flowering plants include bees. Pollinator bees are very sensitive to a particular diet source and combination of nutrients (Harmon-Threatt and Kremen 2015), such as the ratio of various essential amino acids (EAA) to carbohydrates and show poor growth and survival when reared on monotype or non-optimal nutrition diets (Vanbergen et al. 2018). It was found that the protein content of pollen varies with the plant species (Roulston et al. 2000), which influences the pollen-feeding behaviour of bees (Cook et al. 2003; Keller et al. 2005). The reduction or elimination of specialised partner plant populations is particularly important for certain solitary bee species that have specialised relationships with flowering plants (Mueller and Kuhlmann 2008). It is also known that even generalist bee species (which often benefit from abundant resources of mass-flowering invasive plants; Stout and Morales (2009)) require diverse sources of floral pollen, because pollen from different plant species varies in digestibility and nutrient content (Roulston et al. 2000). In our research, we found that bees are almost as sensitive to *S. tomentosa* invasion as butterflies. In dense populations of the shrub, a reduction in the number of bees by 60% was recorded and bee species richness decreased by 70%, which indicates that *S. tomentosa*, despite the large supply of pollen, which constitutes the majority of bee nutrition (Stout and Morales 2009), seems not to be attractive for this group of insects. It is worth noting that the response of bee populations to the presence of *S. tomentosa* in the ecosystem seems to be different in the area of the natural occurrence of the shrub and outside it. In North America, *S. tomentosa* offers both pollen and nectar as pollinator rewards and it is recognised as a species that attracts bumblebees (LaRosa et al. 2004). In Europe, the shrub provides only pollen, which may reduce its attraction to flower visitors looking for nectar. The differences between resources provided by *S. tomentosa* flowers in its native range and in invaded areas may be a result of the pollinator density differences between these areas (Muñoz and Cavieres 2008) or the lack of adaptation to obtaining flower reward (e.g. Liu and Pemberton 2009). However, the latter is unlikely in the case of *S. tomentosa* flowers, which are morphologically similar to flowers of other *Spiraea* species that naturally occur in Central Europe (Mirek et al. 2002).

Another important order amongst insects pollinating flowers around the world are flies from the Syrphidae, Bombyliidae and Muscoidea families (Larson et al. 2001), but also other erroneously overlooked Diptera pollinators (Ssymank et al. 2008; Orford et al. 2015). Amongst all the studied groups of pollinators, flies are the least specialised in flowers, because even though they use pollen and nectar, they also use other food sources (Brock 2015). Additionally, for this group of potential pollinators, a negative effect of *S. tomentosa* coverage on their number and diversity was revealed, but with the lowest impact. In dense populations of this shrub, a reduction in the number of individuals by 45% and reduction in species richness by 30% were found, which may result from the lowest dependence on a specific food source, but also from their greatest mobility amongst the studied groups of insects (Van Veen 2004). Unlike bees, whose females build nests for their offspring and are associated with them because they procure larval cells in the nest, expand it and sleep in it (Batra 1984), many flies have great power of dispersal spread and they are found far from their site of development (Ssymank 2001; Van Veen 2004).

For all the studied groups of potential pollinators, it was found that the influence of *S. tomentosa* is proportional to its density coverage. The number of individuals and richness of butterflies and moths, bees and flies significantly, linearly decreased with the increase in the steeplebush cover, which supports the thesis that the impact, at least of some invasive plants, is proportional to invader population density (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017). Moreover, the potential pollinator community assemblages seem to be affected as *S. tomentosa* cover increases (Fig. 4). Changes in the community assemblages are a result of species loss rather than the constitution of new communities by species replacement. Thus, in areas highly impacted by invasive steeplebush, only a part of the original pool of species can persist. The next step should be to identify traits which make some species less vulnerable to biological invasions (Moroń et al. 2021).

Most studies indicate that the impact of invasive species on potential pollinators depends on whether the invasive species reduces resources, upon which the native species depends and also whether it acts as a novel resource for the native species (Bradley et al. 2019). In the case of the goldenrod (*Solidago canadensis*) invasion, it has been found that this plant reduces the resources, on which native pollinator species depend (it has a linear negative effect on plants). At the same time, it is also a food source for some butterflies and bees (Fenesi et al. 2015), which can cause a buffering effect and result in a non-linear plant impact on pollinators (Moroń et al. 2019). In the case of *S. tomentosa*, we found that this shrub is highly competitive with native plant species and displaces species of wet meadows, which reduces the resources available to native pollinators. Moreover, despite the large supply of pollen steeplebush is not attractive for most pollinators (Wiatrowska et al. 2018a), it does not have compensating properties that would buffer the displacement of native species, which is manifested in a strong, negative, linear response of potential pollinators to *S. tomentosa* invasion.

Conclusions

Effective nature conservation and management of invasive plant species should be based on a comprehensive understanding of the role they play in our ecosystems (Barney 2016). We found that *S. tomentosa* invasion in the wetland ecosystem has a very strong negative effect on the populations of plants and potential pollinators. In the areas invaded by this shrub, only a small part of the native species pool may persist, which implies that *S. tomentosa* should be considered as a transformer species.

The number and diversity of plants, butterflies and moths, bees and flies change at all points in the *S. tomentosa* invasion pathway (representing a linear response to invasion). Although it was assumed that invasive plant impacts are highly scale-dependent (Powell et al. 2013; Rejmánek and Stohlgren 2015), our study is the first to show such an unequivocal negative, linear effect of an invasive species impact on the abundance and diversity of potential pollinators.

Many studies showed that the management effort in the case of invasive species populations largely depends on the density–impact curve of the species and optimisation of management relies on minimising the sum of the costs of their impact and management (Yokomizo et al. 2009). For a linear effect of *S. tomentosa* on plants and potential pollinators, it can be expected that the benefits of controlling this plant will be proportional to the effort involved. As the strong negative impact of this shrub population is observed even at a small density of its population, the control of this plant population at the initial stage of invasion, before its indiscriminate spreading, seems to be the best and most promising approach.

Acknowledgements

This research was financially supported by the statutory activities of the Faculty of Forestry, the Poznań University of Life Sciences and partially financed by National Science Centre's grant (UMO-2020/37/B/NZ8/01743) for Dawid Moroń.

References

Acharya RS, Leslie T, Fitting E, Burke J, Loftin K, Joshi NK (2021) Color of pan trap influences sampling of bees in livestock pasture ecosystem. Biology 10(5): 445–445. https://doi.org/10.3390/biology10050445

Ågren J (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology 77(6): 1779–1790. https://doi.org/10.2307/2265783

Albrecht M, Padrón B, Bartomeus I, Traveset A (2014) Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks. Proceedings of the Royal Society B: Biological Sciences 281(1788): e20140773. https://doi.org/10.1098/rspb.2014.0773

Altermatt F, Pearse IS (2011) Similarity and specialization of the larval versus adult diet of European butterflies and moths. American Naturalist 178(3): 372–382. https://doi.org/10.1086/661248

Balkenhol B, Haase H, Gebauer P, Lehmitz R (2018) Steeplebushes conquer the countryside: Influence of invasive plant species on spider communities (Araneae) in former wet meadows. Biodiversity and Conservation 27(9): 2257–2274. https://doi.org/10.1007/s10531-018-1536-8

Banaszak J, Cierzniak T, Szymański R (1994) Influence of colour of Moericke traps on numbers and diversity of collected bees (Apoidea, Hymenoptera). Acta Universitatis Lodziensis. Folia Zoologica 2: 29–35.

Barney JN (2016) Invasive plant management must be driven by a holistic understanding of invader impacts. Applied Vegetation Science 19(2): 183–184. https://doi.org/10.1111/avsc.12239

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant–pollinator networks. Oecologia 155(4): 761–770. https://doi.org/10.1007/s00442-007-0946-1

Bartoń K (2022) Multi-model inference. Package "MuMIn". https://cran.r-project.org/web/packages/MuMIn/index.html

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J, Bauer A, Krivitsky PN (2022) Linear mixed-effects models using "Eigen" and S4. https://cran.r-project.org/web/packages/lme4/index.html

Batra SW (1984) Solitary bees. Scientific American 250(2): 120–127. https://doi.org/10.1038/scientificamerican0284-120

Bělìn V (1999) Motyli Českě a Slovenskě Republiky Aktivnì ve Dne. Nakladatelství Kabourek, Zlìn, 100 pp.

Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. Annual Review of Entomology 59(1): 119–141. https://doi.org/10.1146/annurev-ento-011613-162104

Bieroński J, Pawlak W, Tomaszewski J (2000a) Commentary on the hydrographic map. Scale 1:50 000. Sheet M-33-19-C Gozdnica, GEOPOL, Poznan.

Bieroński J, Pawlak W, Tomaszewski J (2000b) Commentary on the hydrographic map. Scale 1:50 000. Sheets: M-33-31-A Pieńsk, M-33-30-B Niesky, GEOPOL, Poznan.

Bjerknes A-L, Totland O, Hegland SJ, Nielsen A (2007) Do alien plant invasions really affect pollination success in native plant species? Biological Conservation 138(1–2): 1–12. https://doi.org/10.1016/j.biocon.2007.04.015

Bogusch P, Straka J (2012) Review and identification of the cuckoo bees of Central Europe (Hymenoptera: Halictidae: *Sphecodes*). Zootaxa 3311(1): 1–41. https://doi.org/10.11646/zootaxa.3311.1.1

Borański M (2015) Methodology of Biodiversity Assessment of Pollinating Insects. Apiculture Department Plant Pollination Laboratory, Skierniewice, 6 pp.

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CBJ (2019) Disentangling the abundance–impact relationship for invasive species. Proceedings of the National Academy of Sciences of the United States of America 116(20): 9919–9924. https://doi.org/10.1073/pnas.1818081116

Briscoe AD, Chittka L (2001) The evolution of color vision in insects. Annual Review of Entomology 46(1): 471–510. https://doi.org/10.1146/annurev.ento.46.1.471

Brock PD (2015) A Comprehensive Guide to Insects of Britain and Ireland. Pisces Publications, Newbury.

Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83(8): 2328–2336. https://doi.org/10.1890/0012-9658(2002)083[2328:CFPBAI]2.0.CO;2

Bruus M, Damgaard C, Nielsen KE, Nygaard B, Strandberg B (2007) Terrestriske Naturtyper 2006. NOVANA. Danmarks Miljøundersøgelser. Aarhus Universitet. Faglig rapport fra DMU nr. 643. http://www.dmu.dk/Pub/FR643.pdf [Accessed on 10.06.2022]

Burke VJ, Gibbons JW (1995) Terrestrial Buffer Zones and Wetland Conservation: A Case Study of Freshwater Turtles in a Carolina Bay. Conservation Biology 9(6): 1365–1369. https://doi.org/10.1046/j.1523-1739.1995.09061365.x

Buszko J, Masłowski J (2008) Butterflies of Poland (Lepidoptera: Hesperioidea, Papilionoidea). Koliber, Nowy Sącz, 274 pp.

Campbell JW, Hanula JL (2007) Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. Journal of Insect Conservation 11(4): 399–408. https://doi.org/10.1007/s10841-006-9055-4

Celary W (2005) Melittidae (Hymenoptera: Apoidea: Antophila) of Poland – Their Biodiversity and Biology. Publishing house of the Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Cracow, 175 pp.

Chittka L, Schürkens S (2001) Successful invasion of a floral market. Nature 411(6838): 653. https://doi.org/10.1038/35079676

Coley PD, Bateman ML, Kursar TA (2006) The effects of plant quality on caterpillar growth and defense against natural enemies. Oikos 115(2): 219–228. https://doi.org/10.1111/j.2006.0030-1299.14928.x

Cook SM, Awmack CS, Murray DA, Williams IH (2003) Are honey bees' foraging preferences affected by pollen amino acid composition? Ecological Entomology 28(5): 622–627. https://doi.org/10.1046/j.1365-2311.2003.00548.x

Cronk QCB, Fuller JL (1995) Plant Invaders: the Threat to Natural Ecosystems. Chapman and Hall, London, 256 pp.

Dajdok Z, Nowak A, Danielewicz W, Kujawa-Pawlaczyk J, Bena W (2011) Nobanis – Invasive Alien Species Fact Sheet – *Spiraea tomentosa*. Online Database of the European Network on Invasive Alien Species. www.nobanis.org [Accessed on 03.05.2022]

Dathe HH (1980) Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea, Colletidae). Mitteilungen aus dem Zoologischen Museum in Berlin 56(2): 207–294.

Davidson N (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65(10): 934–941. https://doi.org/10.1071/MF14173

Davis SL, Cipollini D (2014) Do mothers always know best? Oviposition mistakes and resulting larval failure of *Pieris virginiensis* on *Alliaria petiolata*, a novel, toxic host. Biological Invasions 16(9): 1941–1950. https://doi.org/10.1007/s10530-013-0637-2

Dibble KL, Pooler PS, Meyerson LA (2013) Impacts of plant invasions can be reversed through restoration: A regional meta-analysis of faunal communities. Biological Invasions 15(8): 1725–1737. https://doi.org/10.1007/s10530-012-0404-9

Dietzsch AC, Stanley DS, Stout JC (2011) Relative abundance of an invasive alien plant affects native pollination processes. Oecologia 167(2): 469–479. https://doi.org/10.1007/s00442-011-1987-z

Disney RHL, Erzinclioglu YZ (1982) Collecting methods and the adequacy of attempted fauna surveys, with reference to the Diptera. Field Studies, London 5(4): 607–621.

Dormann CF, Fruend J, Gruber B (2022) Bipartite: Visualising Bipartite Networks and Calculating Some (Ecological) Indices. https://cran.r-project.org/web/packages/bipartite/index.html

Duelli P, Obrist MK, Schmatz DR (1999) Biodiversity evaluation in agricultural landscapes: Above-ground insects. Agriculture, Ecosystems & Environment 74(1–3): 33–64. https://doi.org/10.1016/S0167-8809(99)00029-8

Ehrlich PR, Raven PH (1964) Butterflies and plants: A study in coevolution. Evolution 18(4): 586–608. https://doi.org/10.2307/2406212

Elgersma KJ, Ehrenfeld JG (2011) Linear and non-linear impacts of a non-native plant invasion on soil microbial community structure and function. Biological Invasions 13(3): 757–768. https://doi.org/10.1007/s10530-010-9866-9

Faber-Langendoen D [Ed.] (2001) Plant Communities of the Midwest: Classification in an Ecological Context. Association for biodiversity information. Plant Community (Association) Descriptions, Arlington, 705 pp.

Fenesi A, Vágási CI, Beldean M, Földesi R, Kolcsár LP, Shapiro JT, Török E, Kovács-Hostyánszki A (2015) *Solidago canadensis* impacts on native plant and pollinator communities in different-aged old fields. Basic and Applied Ecology 16(4): 335–346. https://doi.org/10.1016/j.baae.2015.03.003

Fiek E (1881) Flora von Schlesien Preussischen und Österreichischen Antheils, Enthaltend die Wildwachsenden, Verwilderten und Angebauen Phanerogamen und Gefass-Cryptogamen. Unter Mitwirkung von Rudold von Uechtritz. J.U, Breslau, 571 pp.

Fletcher RA, Brooks RK, Lakoba VT, Sharma G, Heminger AR, Dickinson CC, Barney JN (2019) Invasive plants negatively impact native, but not exotic, animals. Global Change Biology 25(11): 3694–3705. https://doi.org/10.1111/gcb.14752

Flora of North America (2022) Flora of North America. http://beta.floranorthamerica.org [Accessed on 10.12.2022]

Floyd DA, Anderson JE (1987) A comparison of three methods for estimating plant cover. Journal of Ecology 75(1): 221–228. https://doi.org/10.2307/2260547

Forest Data Bank (2022) Forest Data Bank. https://www.bdl.lasy.gov.pl/portal/ [Accessed on 10.02.2022]

Gilbert B, Levine JM (2013) Plant invasions and extinction debts. Proceedings of the National Academy of Sciences of the United States of America 110(5): 1744–1749. https://doi.org/10.1073/pnas.1212375110

Hardtke HJ, Ihl A (2000) Atlas der Farn und Samenpflanzen Sachsens. Sächsisches Landesamt für Umwelt und Geologie. Materialen zu Naturschutz und Landschaftspflege, Dresden, 806 pp.

Harmon-Threatt AN, Kremen C (2015) Bumble bees selectively use native and exotic species to maintain nutritional intake across highly variable and invaded local floral resource pools. Ecological Entomology 40(4): 471–478. https://doi.org/10.1111/een.12211

Hartig F, Lohse L (2022) Residual diagnostics for hierarchical (multilevel/mixed) regression models. Package "DHARMa". https://cran.r-project.org/web/packages/DHARMa/DHARMa.pdf

Hejda M, Pysek P, Jarosik V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97(3): 393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Invasive species of Belgium (2022) *Spiraea tomentosa*. https://ias.biodiversity.be/species/show/140 [Accessed 11.02.2022]

Karsholt O, Razowski J (1996) The Lepidoptera of Europe. A distributional checklist. Stenstrup: Apollo Books, 382 pp.

Keller I, Fluri P, Imdorf A (2005) Pollen nutrition and colony development in honey bees: Part I. Bee World 86(1): 3–10. https://doi.org/10.1080/0005772X.2005.11099641

Kercher SM, Frieswyk CB, Zedler JB (2003) Effects of sampling teams and estimation methods on the assessment of plant cover. Journal of Vegetation Science 14(6): 899–906. https://doi.org/10.1111/j.1654-1103.2003.tb02223.x

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings. Biological Sciences 247(1608): 303–313. https://doi.org/10.1098/rspb.2006.3721

Kuznetsova A, Brockhoff PB, Christensen RHB, Jensen SP (2022) Tests in linear mixed effects models. Package "lmerTest". https://cran.r-project.org/web/packages/lmerTest/index.html

LaRosa RJ, Rogers DA, Rooney TP, Waller DM (2004) Does Steeplebush (*Spiraea tomentosa*) facilitate pollination of virginia meadow beauty (*Rhexia virginica*)? Michigan Botanist 43(1): 57–62. https://corescholar.libraries.wright.edu/biology/67

Larson B, Kevan P, Inouye D (2001) Flies and flowers: Taxonomic diversity of anthophiles and pollinators. Canadian Entomologist 133(4): 439–465. https://doi.org/10.4039/Ent133439-4

Larson DL, Royer R, Royer MR (2006) Insect visitation and pollen deposition in an invaded prairie plant community. Biological Conservation 130(1): 148–159. https://doi.org/10.1016/j.biocon.2005.12.009

Lenda M, Skórka P, Moroń D (2010) Invasive alien plant species – A threat or an opportunity for pollinating insects in agricultural landscapes? In: Lee TH (Ed.) Agricultural Economics: new Research. Nova Science Publishers, New York, 67–87.

Lenda M, Witek M, Skórka P, Moroń D, Woyciechowski M (2013) Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. Biological Invasions 15(11): 2403–2414. https://doi.org/10.1007/s10530-013-0461-8

Liu H, Pemberton RW (2009) Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive *Solanum*. Oecologia 159(3): 515–525. https://doi.org/10.1007/s00442-008-1232-6

López-Núñez FA, Heleno RH, Ribeiro S, Marchante H, Marchante E (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. Ecology 98(3): 782–793. https://doi.org/10.1002/ecy.1701

Lüdecke D (2022) Create Tidy Data Frames of Marginal Effects for 'ggplot' from Model Outputs. https://cran.r-project.org/web/packages/ggeffects/index.html

Mason TJ, French K (2007) Management regimes for a plant invader differentially impact resident communities. Biological Conservation 136(2): 246–259. https://doi.org/10.1016/j.biocon.2006.11.023

Mazon M, Bordera S (2008) Effectiveness of two sampling methods used for collecting Ichneumonidae (Hymenoptera) in the Cabaneros National Park (Spain). European Journal of Entomology 105(5): 879–888. https://doi.org/10.14411/eje.2008.116

Mazurczyk T, Brooks RP (2021) Native biodiversity increases with rising plant invasions in temperate, freshwater wetlands. Wetlands Ecology and Management 30(1): 139–160. https://doi.org/10.1007/s11273-021-09842-4

Mirek Z, Piękoś-Mirkowa H, Zając A, Zając M (2002) Flowering Plants and Pteridophytes of Poland. A checklist. Biodiversity of Poland (Vol. 1). W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow, 442 pp.

Moodley D, Angulo E, Cuthbert RN, Leung B, Turbelin A, Novoa A, Kourantidou M, Heringer G, Haubrock PJ, Renault D, Robuchon M, Fantle-Lepczyk J, Courchamp F, Diagne C (2022) Surprisingly high economic costs of biological invasions in protected areas. Biological Invasions 24(7): 1995–2016. https://doi.org/10.1007/s10530-022-02732-7

Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122(4): 611–619. https://doi.org/10.1016/j.biocon.2004.09.015

Moroń D, Szentgyörgyi H, Wantuch M, Celary W, Westphal C, Settele J, Woyciechowski M (2008) Diversity of wild bees in wet meadows: Implications for conservation. Wetlands 28(4): 975–983. https://doi.org/10.1672/08-83.1

Moroń D, Skórka P, Lenda M, Kajzer-Bonk J, Mielczarek Ł, Rożej-Pabijan E, Wantuch M (2019) Linear and non-linear effects of goldenrod invasions on native pollinator and plant populations. Biological Invasions 21(3): 947–960. https://doi.org/10.1007/s10530-018-1874-1

Moroń D, Marjańska E, Skórka P, Lenda M, Woyciechowski M (2021) Invader-pollinator paradox: Invasive goldenrods benefit from large size pollinators. Diversity & Distributions 27(4): 632–641. https://doi.org/10.1111/ddi.13221

Mueller A, Kuhlmann M (2008) Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. Biological Journal of the Linnean Society 95(4): 719–733. https://doi.org/10.1111/j.1095-8312.2008.01113.x

Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96(3): 459–467. https://doi.org/10.1111/j.1365-2745.2008.01361.x

Mustajarvi K, Siikamaki P, Rytkonen S, Lammi A (2001) Consequences of plant population size and density for plant–pollinator interactions and plant performance. Journal of Ecology 89(1): 80–87. https://doi.org/10.1046/j.1365-2745.2001.00521.x

O'Connor RS, Kunin WE, Garratt MP, Potts SG, Roy HE, Andrews C, Jones CM, Peyton JM, Savage J, Harvey MC, Morris RKA, Roberts SPM, Wright I, Vanbergen AJ, Carvell C (2019) Monitoring insect pollinators and flower visitation: The effectiveness and feasibility of different survey methods. Methods in Ecology and Evolution 10(12): 2129–2140. https://doi.org/10.1111/2041-210X.13292

GBIF (2022) Global Biodiversity Information Facility. https://doi.org/10.15468/dl.uou3h7 [Accessed on 12.02.2022]

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wanger H (2022) Vegan: community ecology package. https://cran.r-project.org/web/packages/vegan/index.html

Orford KA, Vaughan IP, Memmott J (2015) The forgotten flies: the importance of non-syrphid Diptera as pollinators. Proceedings of the royal society B: biological sciences 282(1805): e20142934. https://doi.org/10.1098/rspb.2014.2934

Panetta F, Gooden B (2017) Managing for biodiversity: Impact and action thresholds for invasive plants in natural ecosystems. NeoBiota 34: 53–66. https://doi.org/10.3897/neobiota.34.11821

Pawlikowski T, Celary W (2003) Keys for Marking Polish Insects, part 24. Hymenoptera. Booklet 68a. Bees – Apidae. Introduction and the subfamily sticky – Colletinae. Polish Entomological Society, Toruń, 66 pp.

Pearson DE (2009) Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. Oecologia 159(3): 549–558. https://doi.org/10.1007/s00442-008-1241-5

Pesenko YuA, Banaszak J, Radchenko VG, Cierzniak T (2000) Bees of the Family Halictidae (excluding *Sphecodes*) of Poland: Taxonomy, Ecology, Bionomics. University Publishing House of the Pedagogical University in Bydgoszcz, Bydgoszcz, 348 pp.

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P (2003) Linking bees and flowers: How do floral communities structure pollinator communities? Ecology 84(10): 2628–2642. https://doi.org/10.1890/02-0136

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: Trends, impacts and drivers. Trends in Ecology & Evolution 25(6): 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Powell KI, Chase JM, Knight TM (2013) Invasive plants have scale-dependent effects on diversity by altering species–area relationships. Science 339(6117): 316–318. https://doi.org/10.1126/science.1226817

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. Global Change Biology 18(5): 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Pyšek P, Hulme PE, Simberlof D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

QGIS Development Team (2022) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Development Core Team (2022) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reis V, Hermoso V, Hamilton SK, Ward D, Fluet-Chouinard E, Lehner B, Linke S (2017) A global assessment of inland wetland conservation status. Bioscience 67(6): 523–533. https://doi.org/10.1093/biosci/bix045

Rejmánek M, Stohlgren TJ (2015) Scale-dependent impact of invasive species: A reply to Chase et al. Biology Letters 11(8): e20150402. https://doi.org/10.1098/rsbl.2015.0402

Reschke C (1990) Ecological Communities of New York State. New York Natural Heritage Program. New York State Department of Environmental Conservation, Latham, 96 pp.

Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JT, Catford JA, Dick JTA, Hulme PE, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Meyerson LA, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Vilà M, Wardle DA (2021) Four priority areas to advance invasion science in the face of rapid environmental change. Environmental Reviews 29(2): 119–141. https://doi.org/10.1139/er-2020-0088

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity & Distributions 6(2): 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Roulston TH, Cane JH, Buchmann SL (2000) What governs protein content of pollen: Pollinator preferences, pollen-pistil interactions, or phylogeny? Ecological Monographs 70(4): 617–643. https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2

Rutkowski L (2011) The Key to Determining the Vascular Plants of the Polish Lowland. Polish Scientific Publishers PWN, Warsow, 814 pp.

Rzechowski J (1994) Surface geological formations. Scale 1: 1,500,000. Worksheet 21.1. In: Najgrakowski M (Ed.) Atlas of the Republic of Poland. E. Romera Polish Cartographic Publishers, S.A.,Warsaw.

Schafale MP, Weakley AS (1990) Classification of the Natural Communities of North Carolina. Third approximation. North Carolina Natural Heritage Program. Division of Parks and Recreation, Department of Environment and Natural Resources, Raleigh, 321 pp.

Scheuchl E (2006) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band II: Megachilidae und Melittidae. 2 erweiterte Auflage. Apollo Books, Stenstrup, 192 pp.

Schirmel J, Bundschuh M, Entling MH, Kowarik I, Buchholz S (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: A global assessment. Global Change Biology 22(2): 594–603. https://doi.org/10.1111/gcb.13093

Schmid-Egger Ch, Scheuchl E (1997) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band III: Andrenidae. Eigenverlag, Velden, 180 pp.

Schube T (1903) Die Verbreitung der Gefasspflanzen in Schlesien Preussischen und Osterreichischen Antheils. Druck von. R. Nischkovsky, Breslau, 361 pp. https://doi.org/10.5962/bhl.title.9731

Senapathi D, Carvalheiro LG, Biesmeijer JC, Dodson CA, Evans RL, McKerchar M, Morton RD, Moss ED, Roberts SPM, Kunin WE, Potts SG (2015) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. Proceedings of the Royal Society B: Biological Sciences 282(1806): e20150294. https://doi.org/10.1098/rspb.2015.0294

Senapathi D, Goddard MA, Kunin WE, Baldock KC (2017) Landscape impacts on pollinator communities in temperate systems: Evidence and knowledge gaps. Functional Ecology 31(1): 26–37. https://doi.org/10.1111/1365-2435.12809

Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. Ecosphere 9(9): e02415. https://doi.org/10.1002/ecs2.2415

Solon J, Borzyszkowski J, Bidłasik M, Richling A, Badora K, Balon J, Brzezińska-Wójcik T, Chab Ł, Dobrowolski R, Grzegorczyk I, Jodłowski M, Kistowski M, Kot R, Krąż P, Lechnio J, Macias A, Majchrowska A, Malinowska E, Migoń P, Ziaja W (2018) Physico-geographical mesoregions of Poland: Verification and adjustment of boundaries on the basis of contemporary spatial data. Geographia Polonica 91(2): 143–170. https://doi.org/10.7163/GPol.0115

Song BM, Lee CH (2018) Toward a mechanistic understanding of color vision in insects. Frontiers in Neural Circuits 12: 16–16. https://doi.org/10.3389/fncir.2018.00016

Spafford RD, Lortie CJ, Butterfield BJ (2013) A systematic review of arthropod community diversity in association with invasive plants. NeoBiota 16: 81–102. https://doi.org/10.3897/neobiota.16.4190

Speight MCD (2017) Species Accounts of European Syrphidae, Syrph the Net, the Database of European Syrphidae (Diptera) (Vol. 97). Syrph the Net publications, Dublin, 294 pp.

Ssymank A (2001) Vegetation und blütenbesuchende Insekten in der Kulturlandschaft: Pflanzengesellschaften, Blühphänologie, Biotopbindung und Raumnutzung von Schwebfliegen (Diptera, Syrphidae) im Drachenfelser Ländchen sowie Methodenoptimierung und Landschaftsbewertung. Bundesamt für Naturschutz, Bonn, 513 pp.

Ssymank A, Kearns CA, Pape T, Thompson FC (2008) Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity 9(1–2): 86–89. https://doi.org/10.1080/14888386.2008.9712892

Stout JC, Morales CL (2009) Ecological impacts of invasive alien species on bees. Apidologie 40(3): 388–409. https://doi.org/10.1051/apido/2009023

Sukopp H, Starfinger U (1995) *Reynoutria sachalinensis* in Europe and in the Far East: a comparison of the species ecology in its native and adventive distribution range. In: Pyšek P, Prach K, Rejmánek M, Wade M (Eds) Plant invasions – general aspects and special problems. SPB Academic, Amsterdam, 151–159.

Sukopp H, Sukopp U (1988) *Reynoutria japonica* Houtt. in Japan und in Europa. Veröffentlichungen Geobotanischer Institut ETH. Stiftung Rübel Zürich 98: 354–372.

Symes M (1983) Charles Hamilton's Plantings at Painshill. Garden History 11(2): 112–124. https://doi.org/10.2307/1586839

Tallamy DW, Shropshire KJ (2009) Ranking lepidopteran use of native versus introduced plants. Conservation Biology 23(4): 941–947. https://doi.org/10.1111/j.1523-1739.2009.01202.x

Tepedino VJ, Bradley BA, Griswold TL (2008) Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal 28(1): 44–50. https://doi.org/10.3375/0885-8608(2008)28[44:MFOIPI]2.0.CO;2

Thompson JD (2001) How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? Oecologia 126(3): 386–394. https://doi.org/10.1007/s004420000531

Tokarska-Guzik B, Dajdok Z, Zając M, Zając A, Urbisz A, Danielewicz W, Hołdynski C (2012) Plants of Foreign Origin in Poland, with Particular Emphasis on Invasive Species. General Directorate for Environmental Protection, Warsaw, 197 pp.

Trigos-Peral G, Casacci LP, Ślipiński P, Grześ IM, Moroń D, Babik H, Witek M (2018) Ant communities and *Solidago* plant invasion: Environmental properties and food sources. Entomological Science 21(3): 270–278. https://doi.org/10.1111/ens.12304

Tyler T, Karlsson T, Milberg P, Sahlin U, Sundberg S (2015) Invasive plant species in the Swedish flora: Developing criteria and definitions, and assessing the invasiveness of individual taxa. Nordic Journal of Botany 33(3): 300–317. https://doi.org/10.1111/njb.00773

USDA – The Plants Database (2022) Fact Sheet – *Spiraea tomentosa*. http://plants.usda.gov [Accessed 20.07.2022]

Van Der Kooi CJ, Stavenga DG, Arikawa K, Belušič G, Kelber A (2021) Evolution of insect color vision: From spectral sensitivity to visual ecology. Annual Review of Entomology 66(1): 435–461. https://doi.org/10.1146/annurev-ento-061720-071644

Van Hengstum T, Hooftman DA, Oostermeijer JGB, Van Tienderen PH (2014) Impact of plant invasions on local arthropod communities: A meta-analysis. Journal of Ecology 102(1): 4–11. https://doi.org/10.1111/1365-2745.12176

Van Veen M (2004) Hoverflies of Northwest Europe: Identification Keys to the Syrphidae. KNNV Publishing, Utrecht, 247 pp. https://doi.org/10.1163/9789004274495

Vanbergen AJ, Espíndola A, Aizen MA (2018) Risks to pollinators and pollination from invasive alien species. Nature Ecology & Evolution 2(1): 16–25. https://doi.org/10.1038/s41559-017-0412-3

Vrdoljak SM, Samways MJ (2012) Optimising coloured pan traps to survey flower visiting insects. Journal of Insect Conservation 16(3): 345–354. https://doi.org/10.1007/s10841-011-9420-9

Westphal C, Bommarco R, Carré G, Lamborn E, Morison N, Petanidou T, Potts SG, Roberts SPM, Szentgyörgyi H, Tscheulin T, Vaissière BE, Woyciechowski M, Biesmeijer JC, Kunin WE, Settele J, Steffan-Dewenter I (2008) Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monographs 78(4): 653–671. https://doi.org/10.1890/07-1292.1

Wiatrowska B, Danielewicz W (2016) Environmental determinants of the steeplebush (*Spiraea tomentosa* L.) invasion in the Bory Dolnoslaskie Forest. Sylwan 160(8): 696–704.

Wiatrowska B, Michalska-Hejduk D, Dajdok Z (2018a) *Spiraea tomentosa* L. – species information sheet. www.projekty.gdos.gov.pl/igo [Accessed 24/07/2022]

Wiatrowska B, Łukowski A, Karolewski P, Danielewicz W (2018b) Invasive *Spiraea tomentosa*: A new host for monophagous *Earias clorana*? Arthropod-Plant Interactions 12(3): 423–434. https://doi.org/10.1007/s11829-017-9592-7

Wiatrowska B, Pietras M, Kolanowska M, Danielewicz W (2020) Current occurrence and potential future climatic niche distribution of the invasive shrub *Spiraea tomentosa* L. in its native and non-native ranges. Global Ecology and Conservation 24: e01226. https://doi.org/10.1016/j.gecco.2020.e01226

Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo C, Yutani H, Dunnington D, Studio R (2022) Create elegant data visualisations using the grammar of graphics. Package "ggplot2". https://cran.r-project.org/web/packages/ggplot2/index.html

Williams NM, Cariveau D, Winfree R, Kremen C (2011) Bees in disturbed habitats use, but do not prefer, alien plants. Basic and Applied Ecology 12(4): 332–341. https://doi.org/10.1016/j.baae.2010.11.008

Woś A (1999) Climate of Poland. Polish Scientific Publishers PWN, Warsaw, 302 pp.

Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: The value of knowing the density – impact curve. Ecological Applications 19(2): 376–386. https://doi.org/10.1890/08-0442.1

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23(5): 431–452. https://doi.org/10.1080/07352680490514673

Appendix 1

Table A1. List of study sites.

Study sites	The nearest village	Geographical coordinates (DMS)	*S. tomentosa* cover (%)
1	Ruszów	51°23'39"N, 15°09'26"E	80
2	Ruszów	51°23'38"N, 15°09'28"E	40
3	Ruszów	51°23'36"N, 15°09'26"E	40
4	Ruszów	51°23'33"N, 15°09'30"E	50
5	Ruszów	51°23'31"N, 15°09'30"E	50
6	Ruszów	51°23'29"N, 15°09'31"E	30
7	Ruszów	51°23'26"N, 15°09'47"E	70
8	Ruszów	51°23'26"N, 15°09'44"E	60
9	Ruszów	51°23'26"N, 15°09'40"E	40
10	Poświętne	51°22'42"N, 15°14'03"E	90
11	Poświętne	51°22'41"N, 15°13'57"E	100
12	Poświętne	51°22'43"N, 15°13'49"E	100
13	Ołobok	51°18'32"N, 15°15'54"E	5
14	Ołobok	51°18'33"N, 15°15'51"E	10
15	Ołobok	51°18'35"N, 15°15'52"E	0,5
16	Gozdnica	51°24'45"N, 15°04'06"E	100
17	Gozdnica	51°24'44"N, 15°04'04"E	100
18	Gozdnica	51°24'45"N, 15°04'02"E	100
19	Iłowa	51°30'11"N, 15°11'11"E	0
20	Iłowa	51°30'12"N, 15°11'10"E	0
21	Iłowa	51°30'13"N, 15°11'11"E	0
22	Stary Węgliniec	51°17'55"N, 15°11'06"E	20
23	Stary Węgliniec	51°17'55"N, 15°11'03"E	60
24	Stary Węgliniec	51°17'57"N, 15°11'07"E	70
25	Stary Węgliniec	51°17'59"N, 15°11'20"E	40
26	Stary Węgliniec	51°17'59"N, 15°11'22"E	30
27	Stary Węgliniec	51°17'58"N, 15°11'18"E	0

Appendix 2

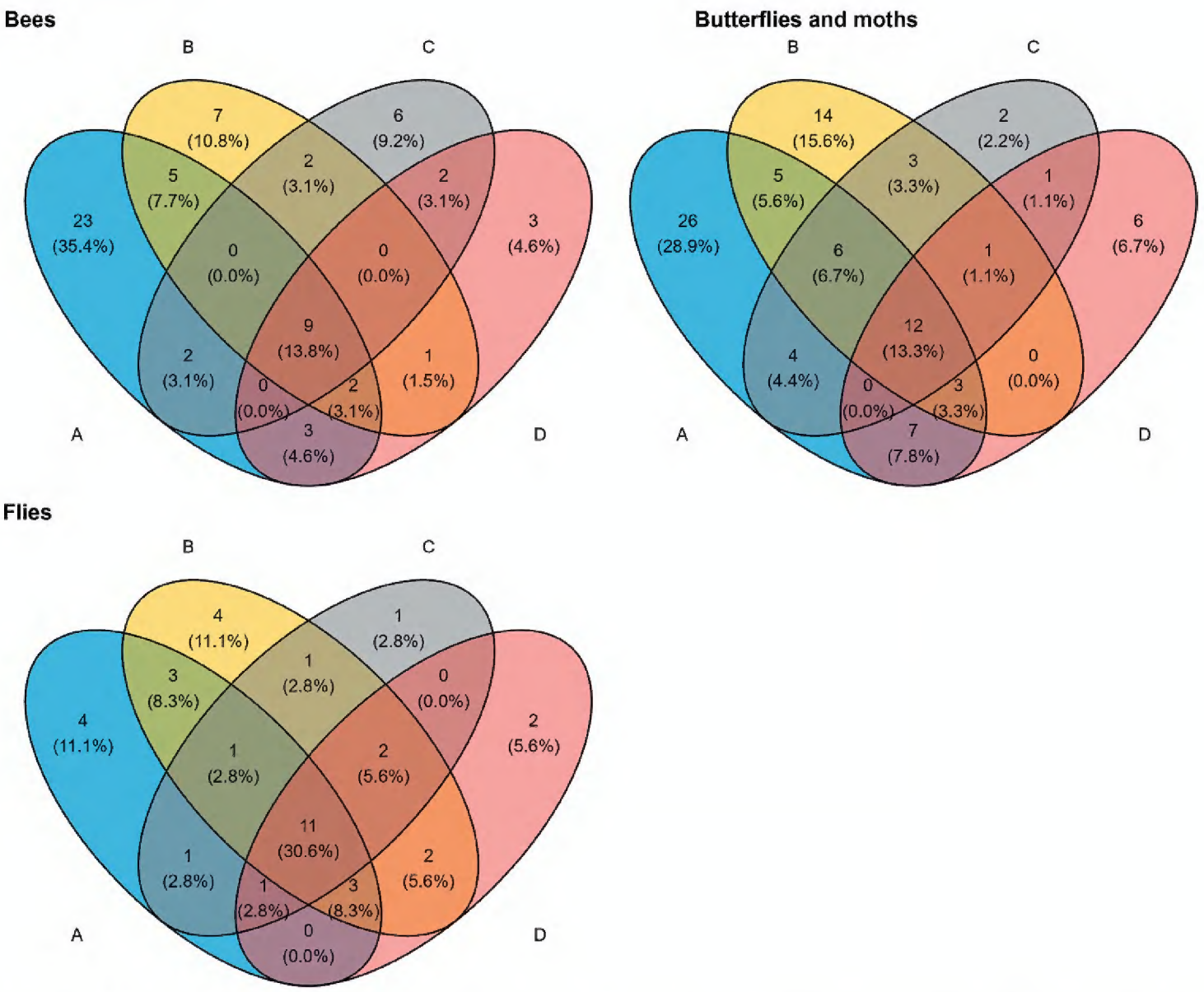

Figure A1. Venn diagrams showing the overlap between bee, butterfly (and moths) and fly species for four classes of *S. tomentosa* cover.